HIGHLIGHTED STUDENT RESEARCH

Snow roosting reduces temperature-associated stress in a wintering bird

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Abstract

Animals in temperate northern regions employ a variety of strategies to cope with the energetic demands of winter. Behavioral plasticity may be important, as winter weather conditions are increasingly variable as a result of modern climate change. If behavioral strategies for thermoregulation are no longer effective in a changing environment, animals may experience physiological stress, which can have fitness consequences. We monitored winter roosting behavior of radio–tagged ruffed grouse (*Bonasa umbellus*), recorded snow depth and temperature, and assayed droppings for fecal corticosterone metabolites (FCM). Grouse FCM levels increased with declining temperatures. FCM levels were high when snow was shallow, but decreased rapidly as snow depth increased beyond 20 cm. When grouse used snow burrows, there was no effect of temperature on FCM levels. Snow burrowing is an important strategy that appears to allow grouse to mediate the possibly stressful effects of cold temperatures. This is one of the first studies to explore how variable winter weather conditions influence stress in a free–living cold–adapted vertebrate and its ability to mediate this relationship behaviorally. Animals that depend on the snowpack as a winter refuge will likely experience increased stress and possible fitness costs resulting from the loss of snow cover due to climate change.

Keywords Behavioral plasticity · Climate change · Ruffed grouse · Fecal corticosterone metabolites · Winter

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Introduction

In temperate and northern regions, winter is a period when animals must balance increased thermoregulatory demands with reduced energy availability and intake (Anderson and Jetz 2005; Williams et al. 2015). While some species avoid winter by migrating (Somveille et al. 2015) or hibernating (Geiser 2013; Sheriff et al. 2011b), others confront the winter through a diversity of physiological adaptations including lowering energy expenditure (Humphries et al. 2005; Sheriff et al. 2009c, d), increasing summit metabolic rates (Cooper 2002), engaging in heterothermy (Dammhahn et al. 2017), or altering morphological features (e.g., increasing fat stores; Pokallus and Pauli 2016). In addition to these physiological responses, overwintering species display a range of behavioral flexibility such as whether or not to cache food (Smith and Reichman 1984), nesting alone or communally (Williams et al. 2013), or seeking out winter refugia, such as within thermally stable areas under the snowpack (Pauli et al. 2013). Flexibility in either physiological or behavioral responses represents a potential capacity for individuals to

respond to shifting environmental conditions (Beever et al. 2017).

Understanding the adaptations of animals that confront the winter is of particular importance as modern climate change is rapidly altering winter conditions. Temperate and northern ecosystems, in particular, are experiencing some of the most rapid changes in temperature (Post 2013). The Great Lakes region of the United States has experienced increasing winter temperatures of 0.5° per decade from 1970 to 2005 (Lorenz et al. 2009) and decreases in snow cover duration, particularly in early spring (Vaughan et al. 2013). These trends have reduced the snow season by 5.3 days per decade since the 1970s (Notaro et al. 2011), a trend that is expected to continue (Krasting et al. 2013). There is growing evidence that changing winter conditions are beyond the capacity of many resident species to respond. For example, reduced snow cover is increasing mismatch in coat color camouflage in snowshoe hares (*Lepus americanus*; (Mills et al. 2013), leading to reduced survival (Wilson et al. 2018; Zimova et al. 2016), and implicated in regional range contraction (Sultaire et al. 2016). When snow is present, rain-on-snow events and increasing freeze–thaw cycles create ice fields that prevent reindeer (*Rangifer tarandus platyrhynchus*) from accessing food below the snow (Hansen et al. 2011). Repeated thawing and refreezing events can be harmful for species that overwinter under the snowpack, such as freeze-tolerant amphibians, as many of these species undergo energy-intensive physiological processes to survive the winter months (Sinclair et al. 2013). Several studies have identified behaviors that help individual species to cope with climate change (Kearney et al. 2009; Snell-Rood 2013), but there is a lack of information on the ecological contexts and consequences of behavioral flexibility in response to climate variability (Beever et al. 2017).

While there is a good understanding of the strategies animals have to cope with cold winter temperatures, relatively less is known about how animals may adapt to variable and changing winter conditions. The study of stress physiology in free-living animals has proven valuable for understanding how vertebrates adjust to environmental change and implement decisions on coping with the challenges of uncertain environments (Dantzer et al. 2014; Sheriff et al. 2011b). Glucocorticoid stress hormones (hereafter, GCs) play critical roles in performance and fitness (Sapolsky et al. 2000; Wingfield et al. 1998) and help animals to cope with and respond to a variety of stressors including food shortages, inclement weather, or increased predator presence. Glucocorticoids are involved in a variety of physiological processes in animals, including cardiovascular activation, immune function, neurobiology, and reproduction (Sapolsky et al. 2000; Wingfield et al. 1998). Glucocorticoids also play a key role in regulating metabolism, and serve to increase circulating concentrations of glucose to provide for an animal's energy needs (Jimeno et al. 2018; Landys et al. 2006; Sapolsky et al. 2000). To enable these functions, GCs can modulate animal behavior by increasing foraging behavior (Astheimer et al. 1992; Nagra et al. 1963; Wingfield and Ramenofsky 1999) or locomotor activity (Astheimer et al. 1992; Breuner et al. 1998; Wingfield and Ramenofsky 1999). However, if an animal cannot escape a stressor, GCs can remain chronically elevated, and can result in significant deleterious effects, including fat depletion and muscle atrophy (Marra and Holberton 1998; Romero and Wikelski 2001) and reduced reproductive output (Sheriff et al. 2009b) and survival (MacLeod et al. 2018a). This could occur either via continual "wear and tear" resulting from elevation of GCs beyond the range of normal seasonal variation (predictive homeostasis), or from extreme elevation into the range of homeostatic overload when the GCs themselves become pathological (Romero et al. 2009).

Elevated GC levels in free-living animals have been associated with inclement weather, and can have fitness consequences. For example, early spring snow storms during the parental care period of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) were associated with greatly elevated corticosterone levels and brood losses (Wingfield et al. 1983). High GC levels were associated with a delayed return to the breeding grounds by mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) that had departed to snow-free lower elevations following spring storms (Hahn et al. 2004). Adelie penguins (*Pygoscelis adeliae*) subjected to experimentally elevated GC levels spent less time incubating eggs, which often led to egg loss, particularly during harsh weather (Thierry et al. 2013). All of these studies occurred during the breeding season, and investigated the interactive effects of harsh weather, stress physiology, and breeding performance. There is almost no information on how changing winter conditions influence stress hormone levels in wild animals (but see Sheriff et al. 2017), and little information on how snow cover and cold temperatures influence the stress physiology of animals adapted to cope with a winter environment.

Ruffed grouse (*Bonasa umbellus*) are winter-adapted birds closely associated with the northern forests of North America, and despite extensive conservation efforts, grouse populations have declined by 50% over the last half century (Rusch et al. 2000). Winter is an important demographic bottleneck for grouse as they experience high rates of mortality, especially via predation (Small et al. 1991; Thompson and Fritzell 1989). Winter precipitation and temperature, in particular, are critical components of grouse dynamics and cycling (Pomara and Zuckerberg 2017). Despite the importance of winter on grouse ecology, it is a relatively understudied portion of their life cycle. During the winter, grouse are typically sedentary and spend up to 80% of the time roosting either on the ground, in trees, or when snow

cover is sufficient, in burrows under the snow (Bump et al. 1947). Snow burrows provide superior thermal insulation as compared to other roost sites (Thompson and Fritzell 1988b). Indeed, snow burrows form microenvironments within thermo-neutral temperatures for grouse (Marjakangas et al. 1984), and are particularly important when grouse have low fat and protein reserves and relatively little metabolic tolerance to fasting (Thomas 1987). Roosting in snow burrows is a potentially important behavioral adaptation that grouse use to maintain energy reserves during harsh winter conditions. Use of snow burrows is primarily limited by the quantity and quality of available snow cover (Gullion 1970), and grouse need roughly 15–20 cm of powdery snow for burrowing (Blanchette et al. 2007; Gullion 1970; Heinrich 2017). Across Wisconsin, which encompasses the southern range boundary for grouse in the Great Lakes region, snow depth averages ~ 10 cm in December and March, and peaks at ~ 20 cm in midwinter when temperatures are coldest (Notaro et al. 2011), resulting in a brief, yet potentially critical, window of time when snow burrowing conditions are suitable.

Here, we tested the hypothesis that both winter temperature and snow depth influence the stress physiology of ruffed grouse, and that behavioral use of snow burrows allow grouse to mediate the influence of temperature on stress hormone levels. Specifically, we predicted (1) corticosterone concentrations (as measured by fecal corticosterone metabolites, FCM) would increase as temperature decreased; (2) corticosterone concentrations would decrease as snow depth and snow compaction depth increased, and (3) ambient temperature would not influence corticosterone concentrations when grouse used snow burrows.

Materials and methods

Study site

Our work was conducted in Sandhill Wildlife Area (44°18′N, 90°07′W), a 3700 ha state wildlife area located in central Wisconsin. Sandhill is a mosaic of naturally fragmented upland oak (*Quercus* sp.) and aspen (*Populus tremuloides* and *P. grandidentata*) forests interspersed by marshes and open water. It is actively managed by the Wisconsin Department of Natural Resources with selective logging to promote habitat for ruffed grouse and white-tailed deer (*Odocoileus virginianus*). Sandhill is surrounded by a 3.5-m-tall fence, and a short 4–5-week ruffed grouse hunting season is limited and closely monitored in the southern half of the wildlife area in autumn. The mean winter temperature at Sandhill (December–March) is − 9 °C ± 10.0 °C (range − 26.5 to 5.5 °C), and between 2001 and 2015, there were on average

47 nights each winter when snow depth exceeded 20 cm (range 0–101 nights).

Grouse trapping and radio telemetry

From Sep-2015 to Nov-2015, we trapped ruffed grouse in walk-in pens ("lily pad traps") located at both ends of a 15-m chicken wire drift fence (Gullion 1965). At capture, we identified age and sex of grouse according to standard criteria (Hale et al. 1954), collected morphological measurements, fitted each bird with an aluminum leg band for identification (National Band and Tag Company), and attached a 12-g necklace-style radio transmitter equipped with a 4-h mortality sensor (Advanced Telemetry Systems, Inc.). During the winter of 2015–2016 (01-Dec to 31-Mar), we located a roost site for each radio-tagged grouse approximately once per week, between 0900 and 1700, typically by flushing the bird off of its roost.

Roost site observations

We categorized roost site locations as "snow roosts" if they occurred in snow burrows [with at least a partial roof of snow (> 75% covered)] or snow bowls (bowl-shaped indentations in the snow without a roof). Alternatively, we used "other roosts" if the grouse were found in trees or sitting on top of the snow or the ground. If a roost location could not be determined during flushing, or there was evidence that the bird was not roosting when it was located (e.g., it was foraging), we relocated the bird 2–3 days later.

We calculated mean snow depth at the roost site by taking the average depth in centimeters from 7 locations that were equidistant from the roost site to the perimeter of a 0.04 ha circular plot: at the roost site, 3.6 m, 7.2 m, and 10.8 m North or South of the roost site, and 3.6 m, 7.2 m, and 10.8 m East or West of the roost site. We measured average snow compaction depth (an index of snow density) at the same 7 locations by dropping a 200-g cylindrical weight with a diameter of 8.5 cm from 50 cm above the top of the snow and recording the sinking depth in cm. Higher values indicate powdery, less dense snow (i.e., increased compaction depth). A value of zero for snow compaction depth indicates very hard snow. If no snow was present, we recorded "N/A" for snow compaction depth.

Fecal sample collection

To estimate grouse stress hormone levels, we collected feces from ruffed grouse roost sites across a roughly 1000-ha area within Sandhill Wildlife Area. Fecal glucocorticoids closely mirror plasma GCs (Sheriff et al. 2010), and provide an accurate non-invasive method for assessing stress in wild populations (Dantzer et al. 2014; Sheriff et al. 2011a).

In black grouse (*Tetrao tetrix*), FCMs peak between 1 and 4 h after administering corticosterone intravenously (Baltic et al. 2005). We collected ruffed grouse fecal droppings from roost sites where individual grouse identity was known with certainty. We attempted to collect all fecal droppings (discarding cecal droppings; Zimmerman et al. 2013) from each roost site. Grouse did not reuse roost sites. All grouse droppings collected from a single roost location (range 2–22 droppings, representing ∼ 1–22 h of roosting time for an individual grouse; (Baltic et al. 2005) were pooled and considered a sample. After collection, fecal samples were immediately put on ice and stored at −20°C for later analysis of corticosterone metabolites. While there is evidence that FCM levels increase artificially when feces are not immediately stored on ice (e.g., Descovich et al. 2012; Khan et al. 2002), in our study, droppings were usually deposited on snow. Additionally, our results show that grouse FCM levels actually decline with warmer temperatures (Fig. 1), further indicating that environmental degradation of samples is not a concern in this study.

Temperature data collection

Temperature data (°C) were recorded at a central location within the study site using an iButton data logger (DS1922L; Maxim Integrated). Temperature readings at 1 m above ground were recorded every 30 min throughout the winter. Minimum temperature from the previous night was used for each grouse roost observation. Minimum nightly temperature likely represents the maximum challenge to a bird's ability to cope with the cold (Frigerio et al. 2004) and also likely a factor influencing initial roost site selection.
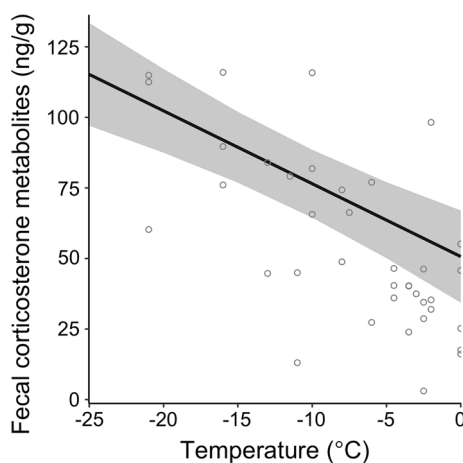

Fig. 1 Partial residual plot of ambient temperature and ruffed grouse fecal corticosterone metabolite concentrations, January–March 2016, Sandhill Wildlife Area, Wood County, WI. Shaded areas represent 95% confidence intervals

Corticosterone assay protocol

We used a standard corticosterone I^{125} double-antibody radioimmunoassay (RIA) kit (MP Biomedicals, Solon, Ohio) to measure corticosterone metabolites (Millspaugh and Washburn 2004; Wasser et al. 2000) that has been validated for use in ruffed grouse (Zimmerman et al. 2013). We followed the manufacturer's instructions for the RIA assay, but halved all reagents (Wasser et al. 2000; Zimmerman et al. 2013). Briefly, we freeze-dried samples using a lyophilizer for 24 h and finely ground and mixed using a mortar and pestle. We extracted corticosterone metabolites by adding 2 ml of 90% methanol to 200 mg of dried feces and vortexing for 30 min. We centrifuged samples at 1900g for 20 min, removed the supernatant, diluted (1:20) with assay buffer, and stored the samples at −20 °C until assayed with the RIA kit. The average intra-assay coefficient of variation was 2.38%. All samples were assayed in a single run; therefore, we did not calculate an inter-assay coefficient of variation.

Statistical analyses

We used a generalized linear mixed-effects model (GLMM) with a Gaussian error distribution (Zuur et al. 2009) to model the effects of environmental conditions and roost type on variation in grouse stress hormone levels. Each model was weighted by the log-transformed number of fecal droppings that were collected at each roost. We used number of droppings as a proxy for length of time that a bird spent at a roost, given that galliformes defecate 1–3 solid feces per hour (Baltic et al. 2005). The longer a bird spent at a roost, the more likely the environmental conditions of the roost would be reflected in its FCM levels. We tested for the effect of minimum temperature, snow depth, snow compaction depth, date, time of day, and roost type as fixed effects. Predictor variables (other than roost type) were scaled using a z-transformation to enable comparisons among predictors (presented as $\beta \pm SE$). Corticosterone metabolite concentrations were log-transformed, and individual bird ID was included as a random effect. We first performed an analysis to test for important environmental variables that influence grouse FCM, independent of grouse roosting behavior. For this first analysis, we developed a list of a priori candidate models (Table 1), which included combinations of 1–5 of the abiotic factors: temperature, snow depth (linear and quadratic forms), compaction depth, date, time of day, and two-way interactions of the above factors. Time of day was included to account for the natural daily rhythm in FCM levels often seen in birds (e.g., Carere et al. 2003; Scheiber et al. 2017). We did not include predictor variables or their interactions in the same model if they exhibited multicollinearity (Pearson's correlation coefficient ≥ 0.6) or

Table 1 Model selection for abiotic factors influencing Ruffed Grouse fecal corticosterone metabolite concentrations, January–March 2016, Sandhill Wildlife Area, Wood County, WI

Model	k	AIC_c	ΔAIC_c	w_i
TEMP + DEPTH^2 + CDEPTH + TIME	8	86.46	0.00	0.34
TEMP + DEPTH^2 + CDEPTH	7	87.48	1.02	0.21
TEMP + DEPTH^2	6	88.80	2.35	0.11
TEMP*CDEPTH	6	88.90	2.44	0.10
TEMP	4	89.82	3.36	0.06
TEMP + DEPTH^2 + TIME	7	90.05	3.59	0.06
TEMP*CDEPTH + TIME	7	91.00	4.54	0.04
TEMP + TIME	5	91.41	4.95	0.03
TEMP + CDEPTH	5	92.05	5.59	0.02

Only models with a $\Delta AIC_c < 6$ are shown. The full list of candidate models can be found in Supplementary Materials

TEMP minimum temperature, *DEPTH* snow depth, *CDEPTH* snow compaction depth, *TIME* time of day, *DATE* date, k number of parameters in the model, AIC_c Akaike's information criterion corrected for small sample sizes, ΔAIC_c change in AIC_c from the model above, w_i Akaike weight

*Interaction

if the model had a variance inflation factor (VIF; measure of the degree of collinearity in a model) greater than five (Dormann et al. 2013). We ranked models based on Akaike's Information Criterion corrected for small sample sizes [AIC$_c$; (Burnham and Anderson 2002)], and models were considered competitive if they were within 2 ΔAIC of the top model. If more than one model was competitive, we selected the model with the greatest AIC weight (w_i) for interpretation. We chose not to use model averaging of parameter estimates for competitive models, given recent concerns about model averaging of parameter estimates in model selection (Cade 2015). After identifying important abiotic factors that influenced grouse FCM (i.e., those variables in the top model), we ran a second analysis to test for the importance of individual grouse

characteristics in mediating the influence of environmental variables on FCM levels. Therefore, in the second analysis, we included all the important environmental factors retained from the first analysis, and included grouse roost type, which included two categories: "snow roost" (snow bowls and snow burrows) and "not snow roost" (all other roost types), grouse age, grouse sex, and two-way interactions with abiotic predictors. We performed a residual analysis to confirm that statistical assumptions were met. We implemented GLMMs using the lme4 package (Bates et al. 2015) and calculated the conditional R^2 (Nakagawa and Schielzeth 2013) for the top model in each round of model selection using the MuMIn package (Barton 2018) in the R statistical platform (R Core Team, ver. 3.3.3). For brevity, we list the candidate models with a $\Delta AIC_c < 6$ in Tables 1 and 2, but for a complete list of candidate models used in both analyses, see the Supplementary Materials (Tables S1 and S2). Using estimates of the between-group variance and within-group variance obtained from our top model, we calculated repeatability (i.e., the proportion of the total variation in FCM levels accounted for by differences between individual grouse; intraclass correlation coefficient) (Roche et al. 2016). We used the non-parametric Mann–Whitney U test to test for differences in environmental variables between snow roosts and other roosts. Mean values are given $\pm$ the standard deviation.

To display the results of our top model, we used the *visreg* function in the *visreg* package to compute partial residuals (Breheny and Burchett 2017). Partial residual plots hold all parameters in the statistical model that are not being displayed constant (at the median value of each parameter). Partial residual plots are an appropriate way to visualize the data because both the plotted points and the model's estimate of the effect of the predictor on the response variable take into account the other variables in the model (Breheny and Burchett 2017; Rohr et al. 2018). Plots with raw data values can be found in Supplementary Materials (Figs. S5–S7).

Table 2 Model selection for abiotic and biotic factors influencing Ruffed Grouse corticosterone metabolite concentrations, January–March 2016, Sandhill Wildlife Area, Wood County, Wisconsin, USA

Model	k	AIC_c	ΔAIC_c	w_i
TEMP*ROOST + DEPTH^2 + CDEPTH + TIME	10	80.63	0.00	0.65
TEMP*ROOST + ROOST*DEPTH^2 + CDEPTH + TIME	12	84.89	4.25	0.08
TEMP + DEPTH^2 + CDEPTH + TIME + SEX	9	85.62	4.99	0.05
TEMP + DEPTH^2 + CDEPTH + TIME + AGE	9	85.72	5.09	0.05
TEMP + DEPTH^2 + CDEPTH + TIME	8	86.46	5.83	0.04

Only models with a $\Delta AIC_c < 6$ are shown. The full list of candidate models can be found in Supplementary Materials

TEMP minimum temperature, *DEPTH* snow depth, *CDEPTH* snow compaction depth, *TIME* time of day, *ROOST* roost type, *SEX* grouse sex, *AGE* grouse age, k number of parameters in the model, AIC_c Akaike's information criterion corrected for small sample sizes, ΔAIC_c change in AIC_c from the model above, w_i Akaike weight

*Interaction

Results

We measured fecal corticosterone metabolites in droppings collected from 70 roost sites used by ruffed grouse during Jan-2016–Mar-2016 (Fig. S1). We created a subset of the dataset for subsequent analysis to only include data points with values for snow compaction depth (i.e., snow depth > 0 cm). Further, at five roost sites, we did not record the number of fecal droppings that we collected, and these observations were removed so that all observations in the final dataset could be weighted by number of droppings. Our final dataset included fecal samples from 50 roost sites (15 snow roosts and 35 other roosts; roost sites were never re-used by individual grouse), representing 15 radio-tagged individuals. The mean number of samples (i.e., roost sites) per individual grouse was 3.3 (range: 2–5). The number of droppings at roosts ranged from 2 to 22 ($\bar{x} = 11.04 \pm 6.09$). Minimum air temperature ranged from -26.5 to 2.0 °C ($\bar{x} = -10.4 \pm 9.3$ °C; Fig. S2). Snow depth ranged from 2.4–39.6 cm ($\bar{x} = 21.0 \pm 10.5$ cm; 27 out of all 50 roost sites (including all roost types) we observed had snow depths greater than 20 cm). Snow compaction depth ranged from 0 to 9.8 cm ($\bar{x} = 4.6 \pm 3.2$ cm). We included date in the model set as a single predictor to test for a temporal effect of winter conditions that might influence stress levels in grouse, but are not captured by our weather variables (e.g., food availability). Snow depth and snow compaction depth were correlated ($r = 0.77$), but our top models from the first (Table 1) and second rounds (Table 2) of model selection had VIFs less than five (4.17 and 4.42, respectively), and we chose not to exclude snow depth and snow compaction depth from the same models. While we recognize that there is likely a mechanistic relationship between snow compaction depth and temperature, we did not find a statistical correlation in our dataset. The repeatability (proportion of variation in FCM levels due to inter-individual differences between grouse) was 0.00, suggesting that the variation in corticosterone metabolites was due to environmental effects not differences among individual grouse.

Effects of ambient temperature and snow on FCM levels

We found strong support for the role of ambient temperature and snow depth on grouse FCM levels, and the top model included minimum temperature, the quadratic form of snow depth, snow compaction depth, and time of day (AIC$_c$ weight = 0.34; $R^2 = 0.24$; Table 1). An additional competitive model was identical to the top model, but did not include time. FCM concentrations increased as

Table 3 Relationships between fecal corticosterone metabolite concentrations and environmental predictors and roost type for Ruffed Grouse at Sandhill Wildlife Area, Wood County, Wisconsin, USA

Fixed effects	β	SE	95% CI
Intercept	3.86	0.08	3.86, 3.92
TEMP	-0.50	0.08	$-0.50, -0.49$
ROOST	0.15	0.17	0.15, 0.17
DEPTH	-2.43	0.85	$-2.43, -2.35$
DEPTH^2	-1.13	0.44	$-1.14, -1.09$
CDEPTH	0.29	0.11	0.29, 0.31
TIME	-0.11	0.06	$-0.11, -0.10$
TEMP*ROOST	0.55	0.15	0.55, 0.57

Only variables in the top model (based on AIC model selection of a list of generalized linear mixed-effects models) are presented here. Individual bird ID was included as a random effect to control for non-independence among individuals in the population

B beta estimate, *SE* standard error, *95% CI* 95% confidence interval, *TEMP* minimum temperature, *DEPTH* snow depth, *CDEPTH* snow compaction depth, *TIME* time of day, *ROOST* roost type (snow roost = 1, other roost = 0)

*Interaction

ambient temperature became colder (Table 3, Fig. 1), and generally decreased with greater snow depth, but this relationship was nonlinear as evidenced by the inclusion of the quadratic form of snow depth (Table 3, Fig. 2). As snow depth increased to 15 cm, FCM concentrations remained stable, but as snow depth increased beyond 15–20 cm, FCM concentrations rapidly decreased. Contrary to our predictions, and independent of snow depth, there was a positive relationship between snow compaction depth and FCM concentrations (Table 3; Fig. 2). As snow became increasingly powdery and less dense (increased snow compaction depth), grouse FCM concentrations increased. FCM levels were highest earlier in the day (Table 3).

Mediating effects of snow roosting

We found that flexible roosting behavior tended to modify the relationship between grouse FCM levels and winter conditions. The single competitive model obtained from the second round of model selection included time of day, the quadratic of snow depth, snow compaction depth, and an interaction between temperature and roost type (AIC$_c$ weight = 0.65; $R^2 = 0.34$; Table 3). When grouse used snow roosts, there was no effect of temperature on FCM levels, but if they used any other roost type, the strong negative relationship between FCM levels and ambient temperature remained (Fig. 3). At the coldest temperatures (-26.5 °C), roosting in snow burrows reduced grouse FCM levels by 45% (138.15 ng/g in other roosts vs. 74.70 ng/g in snow burrows).
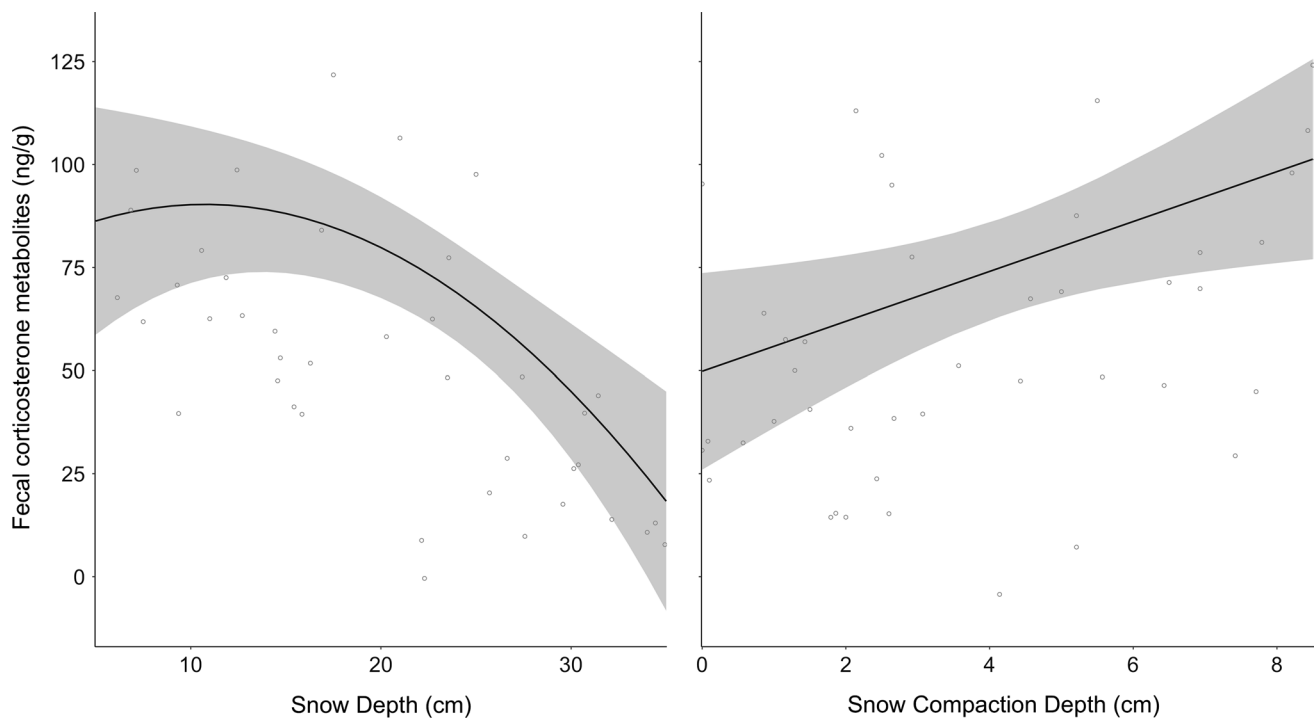
Fig. 2 Partial residual plots of snow depth and snow compaction depth and ruffed grouse fecal corticosterone metabolite concentrations, January–March 2016, Sandhill Wildlife Area, Wood County, WI. Shaded areas represent 95% confidence intervals
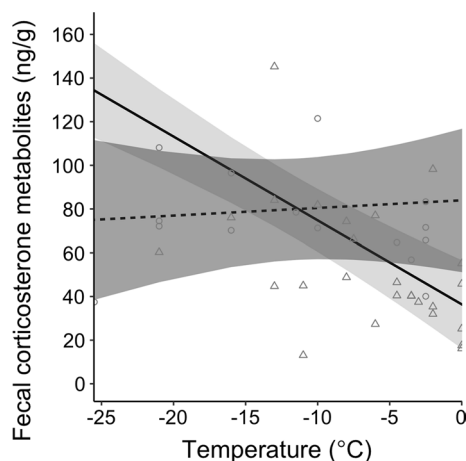

Fig. 3 Partial residual plot of the interaction between ambient temperature and roost site and ruffed grouse fecal corticosterone metabolite concentrations, January–March 2016, Sandhill Wildlife Area, Wood County, WI. The dashed and solid lines indicate the effect of temperature on corticosterone for ruffed grouse using snow roosts vs. using other roosts, respectively. Circles and triangles represent partial residuals for ruffed grouse using snow roosts vs. using other roosts, respectively. Shaded areas represent 95% confidence intervals

Further, we found very similar results when we restricted the dataset to observations with 8 or more fecal droppings ($n = 35$ roost observations): the top model remained the same and the relationships between

FCMs and temperature ($\beta = -0.53$, SE $= 0.09$), roost type ($\beta = 0.10$, SE $= 0.19$, snow depth ($\beta = -2.50$, SE $= 0.80$), the quadratic of snow depth ($\beta = -1.38$, SE $= 0.41$), snow compaction depth ($\beta = 0.42$, SE $= 0.13$), time of day ($\beta = -0.17$, SE $= 0.06$), and the interaction between temperature and roost type ($\beta = 0.62$, SE $= 0.16$) were essentially unchanged (Table 3).

Additionally, we found no differences in minimum temperature or the number of droppings between snow roosts and other roosts. The number of droppings at snow roosts and other roosts ranged from 2 to 21 and 2 to 22, respectively ($\bar{x} = 11.2 \pm 6.3$ and 11.0 ± 6.1 droppings, $W = 254.5$, $p = 0.87$). Minimum air temperature ranged from -25.5 to -2.5 °C and -26.5 to 2.0 °C for snow roosts and other roosts, respectively ($\bar{x} = -11.3 \pm 8.2$ and 10.0 ± 9.8 °C, $W = 293.5$, $p = 0.52$). The numbers of snow roost sites and other roost sites located for each individual grouse are given in Figures S3 and S4, respectively. Snow was deeper at snow roosting sites, ranging from 12.7 to 39.6 cm and 2.4 to 31.4 cm for snow roosts and other roosts, respectively ($\bar{x} = 29.7 \pm 9.0$ cm and 17.3 ± 8.8 cm, $W = 80$, $p < 0.001$). Snow compaction depth was greater (i.e., snow was more powdery) at snow roosting sites, ranging from 1.8 to 9.8 cm and 0 to 9.1 cm for snow roosts and other roosts, respectively ($\bar{x} = 7.2 \pm 2.6$ cm and 3.4 ± 2.7 cm, $W = 84.5$, $p < 0.001$).

Discussion

Our study is a novel exploration of the influence of winter conditions on the stress physiology of a wild bird and the behavioral responses used to mediate such a relationship. We found that wintering ruffed grouse had greater FCM levels (indicative of greater plasma corticosterone levels) when ambient temperatures were low and when snow was shallow. Further, we found that the use of snow burrows eliminated the relationship between ambient temperature and FCM levels, and grouse roosting in snow burrows had lower FCM levels than those roosting outside of snow burrows. For species that overwinter in temperate and northern areas, physiological and behavioral adaptations that maximize energy conservation during winter are critical (e.g., Humphries et al. 2005; Pokallus and Pauli 2016; Sheriff et al. 2009c, d).

The influence of ambient temperature

During the winter season, we found that grouse had higher FCM levels during periods of cold ambient temperatures. We suggest that cold-induced increases in FCM levels are associated with animals' need to increase energy expenditure. For example, corticosterone metabolites in greylag geese (*Anser anser*) increased with decreasing minimum ambient temperature, reflecting the role of corticosterone in thermoregulation (Frigerio et al. 2004). At extreme cold temperatures, more energy is required for thermoregulation, and increases in circulating glucocorticoids may help mediate increased metabolic demand (Jimeno et al. 2018; Sapolsky et al. 2000). For example, in captive birds, variation in GCs has been shown to be a reflection of increased energy expenditure, independent of psychological stress (Jimeno et al. 2018). A changing winter environment, including drops in temperature, combined with loss of snow cover (see below), may increase stress hormone levels as a result of higher metabolic demands for thermoregulation in winter-adapted species.

The mediating effects of snow depth and snow burrow use

Snow cover is a critical seasonal characteristic of many temperate environments, and deep snow was associated with lower FCM levels in grouse, but this relationship was nonlinear. Grouse FCM levels remained stable, but high, as snow depth increased to 15 cm, and rapidly decreased thereafter as snow depth increased beyond 15 cm. Interestingly, ~ 15–20 cm is often cited as the minimum depth required for grouse to use snow burrows (Gullion 1970; Heinrich 2017; Thompson and Fritzell 1988a). As snow depth increases beyond 20 cm, the prevalence and ability to use snow burrows may increase, resulting in lower energetic costs and FCM levels for grouse. When winter temperatures were low, we found that snow burrowing behavior mediated the effect of cold temperatures on FCM levels, and grouse in snow burrows had lower FCM levels than those outside of snow burrows regardless of temperature. For example, during the coldest temperatures we recorded (− 26.5 °C), birds that used snow burrows had 45% lower FCM levels than those that did not. Thus, we believe that the use of snow burrows decouples the strong negative relationship between FCM levels and ambient temperature because it alleviates some of the costs of thermoregulation. However, we acknowledge that there may be important ecological differences between true snow burrows and snow bowls. In this study, we pooled snow burrows and bowls due to a small sample size of burrows (12 snow bowls and 3 snow burrows). True snow burrows are likely even more insulative than snow bowls (which are open on top), and the reduction in FCM levels through the use of true snow burrows is likely even greater than what we documented.

Other northern species have been shown to use behavior to modify their thermoregulatory costs during winter. For example, female red squirrels (*Tamiasciurus hudsonicus*), which are typically asocial, are more likely to nest communally during cold temperatures to conserve heat (Williams et al. 2013). Given that snow burrows can retain more heat and result in temperatures approximately 7 °C warmer than other roost sites (Marjakangas et al. 1984; Thompson and Fritzell 1988a), they likely provide a significant energy savings as reflected in lower grouse FCM levels. The lower critical temperature for ruffed grouse (below which they must increase their metabolic rate to keep up with environmental demands) has been estimated as − 0.3 °C (Rasmussen and Brander 1973) and as 1.5 °C (Thompson and Fritzell 1988a). Given that average winter temperatures were − 10 °C, the use of snow burrows may allow grouse to remain at or close to their lower critical temperature, and within their thermal neutral zone.

An alternative explanation for the reduced corticosterone levels in grouse using snow burrows is the evidence that snow burrows provide a refuge from predators, particularly raptors (Gullion 1970; Heinrich 2017; Marjakangas 1986). Grouse in snow burrows are often completely concealed, and snow that is not deep enough for burrowing may result in grouse being more visible to predators and possibly increase their risk of predation. Perceived risk of predation is associated with greater stress hormone levels in many species (Sheriff et al. 2009b; Sheriff and Thaler 2014), and grouse roosting outside of snow burrows may perceive increased vulnerability. In fact, rock ptarmigan (*Lagopus mutus*) soil their white feathers to become less conspicuous after snow melt and prior to spring molt, indicating the ability to

perceive increased risk due to camouflage mismatch (Montgomerie et al. 2001). While not being in a snow burrow might result in grouse being more exposed to predators, the loss of snow's thermal protection may also increase foraging activities to compensate for energy loss, resulting in the possible synergistic consequences of increased predation risk and energy deficits due to low snow cover. Again, there may be differences in predation risk for birds roosting in true snow burrows and those using snow bowls, and snow burrows likely provide more protection from predators. Similar to the thermoregulatory benefits of snow burrows, if the decrease in FCM levels shown here for birds in snow roosts is due to a decrease in perceived predation risk, this effect is likely to be even greater for grouse using true snow burrows.

We found powdery, uncompacted snow was associated with increased grouse FCM levels, which was unexpected, as grouse need light, powdery snow for burrowing (Blanchette et al. 2007; Gullion 1970). Less dense snow, however, may increase energy expenditure because birds must "snowplow" through deep powdery snow as they walk. The effect of powdery snow may be especially costly when snow is not sufficiently deep for burrowing, but is powdery enough that birds must push their way through it, or resort to flying, which is also energy intensive (Gallagher et al. 2017). The influence of snow quality warrants further exploration.

Interpreting fecal corticosterone metabolite concentrations

There has been much work in assessing the usefulness of FCM concentrations as indicators of plasma GCs in wildlife (Dantzer et al. 2014; Dickens and Romero 2013; Goymann 2012; Sheriff et al. 2011a; Washburn and Millspaugh 2002). However, several confounding factors that can alter FCM levels and limit its usefulness are often overlooked. In our study, factors related to the interaction between sample integrity and environmental temperatures may have influenced FCM levels. For example, it has been shown that fecal samples exposed to rainfall, elevated temperatures (> 22 °C) (Descovich et al. 2012; Khan et al. 2002), or freeze–thaw cycles (Washburn and Millspaugh 2002) can exhibit artificially elevated FCM concentrations. Increased microbial activity due to rain events (Washburn and Millspaugh 2002) or excessive heat (Millspaugh et al. 2003) has been suggested to influence FCM levels. However, these factors are unlikely to have altered our results because we designed our field protocol to avoid sample collection during rainfall, elevated temperatures, or freeze–thaw events. Further, we found that increasing temperatures resulted in lower FCM concentrations, and as a result, if ambient temperature had any effect on our samples, our results would be considered conservative. Ambient temperature may also have affected our FCM concentrations indirectly with lower temperatures

causing animals to increase food intake and ultimately 'diluting' FCM levels because of increased fecal bulk (Goymann 2012); however, the rate of metabolite secretion may be proportional to the rate of fecal excretion (Randall et al. 2000; Sheriff et al. 2009a; Touma et al. 2003; Wasser et al. 1994). If this factor influenced our FCM concentrations, our results would again be a conservative estimate because we would expect our FCM concentrations to be 'diluted' at lower temperatures, but we found that lower temperatures increased FCM concentrations. Finally, it is possible that "baseline" differences in FCMs exist between individual grouse, but repeatability (Roche et al. 2016) was zero, and we found little evidence of appreciable differences in FCMs between individual grouse. Thus, although we believe our methodology accounted for factors that could influence FCM levels, if such factors were influential, our results are a conservative estimate of the influence of temperature on FCM levels and the ability of grouse to behaviorally mediate such a relationship.

Implications of future losses in snow cover

Most studies on the behavioral shifts in response to climate variability focus on directional stimuli (e.g., increases in average summer temperature, earlier spring conditions) and behavioral changes over extended timescales (e.g., multiple seasons) (Beever et al. 2017). For example, many studies have shown that climate-induced advances of spring conditions have created a mismatch between animal phenology and their environment, with potential consequences to fitness (e.g., Both et al. 2006, 2009; Sheriff et al. 2017). However, far fewer studies have investigated animal responses to rapidly shifting and ephemeral climate stressors (i.e., within season changes in temperature and snow cover), which could play an equally important role in species' ability to cope with a changing climate (Beever et al. 2017).

During the winter of 2015–2016, only 27 out of the 70 roost sites we discovered had snow depths greater than 20 cm. Average mid-winter snow depth across Wisconsin currently peaks at 20 cm (Notaro et al. 2011). Future climate projections predict that peak midwinter snow depths will decline to 8–15 cm (Notaro et al. 2011, 2014), with an increase in the number of freeze–thaw events (Mellander et al. 2007; Sinha and Cherkauer 2010) resulting in a shallow and hardened snow layer, which will nearly eliminate the possibility of snow burrowing. A mid-winter thaw resulting in snow melt, followed by low temperatures, may be particularly hazardous, as these winter-adapted birds may lose an important seasonal refuge that allows them to escape cold temperatures and predation. Consequently, while winters are expected to become warmer in the future, the loss of snow cover will result in a functionally colder environment for

many snow-adapted species (Pauli et al. 2013; Zuckerberg and Pauli 2018).

For species that require snow for thermoregulation or to reduce predation risk (e.g., Pauli et al. 2013; Sinclair et al. 2013), or for organisms that molt white in winter for crypsis (Mills et al. 2013), the loss of snow, even for short periods of time, can result in a significant fitness cost via stress hormone-induced reductions in body condition, growth, and immunity (Boonstra 2013). Further, temperature-induced increased energy expenditure for thermoregulation and associated increases in stress hormone levels during the winter may also carry over to increase an individual's vulnerability to subsequent stressors during the breeding season (MacLeod et al. 2018b). Overwintering species have evolved a number of behavioral adaptations in using winter refugia to minimize the physiological consequences of seasonality, but a rapidly changing winter environment and the loss of snow cover could stretch the limits of behavioral flexibility.

Author contribution statement BZ and AAS conceived and designed the study, conducted statistical analyses, and drafted initial versions of the manuscript. AAS collected field data, carried out hormone assays, and led manuscript development. MJS coordinated hormone analysis. JNP provided input on conceptual development. All authors contributed to writing the manuscript and gave final approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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